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Native coffee agroforestry in the Western Ghats of India maintains higher carbon storage and tree diversity compared to exotic agroforestry

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ABSTRACT

The ongoing introduction of the exotic *Grevillea robusta* tree species into agroforestry systems (AFS) of the Indian Western Ghats could become a threat to both climate change mitigation and tree diversity conservation.

Here, we quantified carbon (C) storage and shade tree diversity in native forests and coffee AFS under contrasted management (native versus exotic shade trees, Robusta versus Arabica systems) at 67 plots along a 3500 mm precipitation gradient in the Cauvery watershed, India.

Despite a substantial reduction of shade tree cover in native AFS compared to forest (from 90% to 32% in the high precipitation area), native AFS and forests displayed high and comparable C stocks (max. 228 MgC ha^{-1} and 234 MgC $ha^{-1,}$ respectively) and tree diversity (max. 44 and 45 species, respectively). Both variables were negatively impacted by the introduction of *G. robusta*, especially in Robusta coffee systems (max. 158 MgC ha^{-1}, 12 species).

The current trend toward the introduction of *G. robusta* in coffee AFS of the study area (exotic agroforestry) negatively affects C storage and tree diversity, especially in Robusta coffee systems. Policy makers should take advantage of the carbon-tree diversity positive correlation found in the agroforestry landscape of the Western Ghats of India to promote conservation and climate change mitigation.

1. Introduction

The ongoing deforestation and biodiversity decline caused by human disturbance is strongly affecting the functioning of tropical forests, which may hamper their ability to sustain ecosystem services in the future (Hooper et al., 2012). Indeed, recent studies (e.g. De Beenhouwer et al., 2013; Gibson et al., 2011) highlighted that both biodiversity and ecosystem services are reduced by management intensification (i.e. from native forest to mono-specific plantation or full-sun crops). In this context, agroforestry systems (AFS), where crops or pasture are grown in association with trees, have been proposed as a way to reconcile biodiversity conservation and crucial ecosystem services such as food supply and carbon (C) storage (De Beenhouwer et al., 2016; Nair et al., 2009). In such systems, tree shade is commonly finely tuned through tree planting, thinning and pruning, in order to obtain favourable light and humidity conditions for coffee production (Beer et al., 1997; Tscharntke et al., 2011).

Coffee is an important example of crop traditionally cultivated under native tree shade, with strong benefit for biodiversity conservation and C storage (Perfecto et al., 2014). A current trend toward the use of fast-growing exotic tree monocultures, instead of native canopies, is however currently observed in coffee AFS worldwide (Ehrenbergerová et al., 2016; Nath et al., 2011; Schmitt-Harsh et al., 2012). This simplification of coffee AFS canopies may affect AFS functioning and biodiversity conservation. Tree species identity and diversity has indeed been reported to affect forest carbon and water cycling (Castro-Díez et al., 2012; Kunert et al., 2012; Potvin et al., 2011), as well as the richness and community compositions of other ecosystem components such as birds (Gil-Tena et al., 2007), insects (Sobek et al., 2009) and soil organisms (Tedersoo et al., 2016).

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The simplification of coffee AFS tree species composition has been particularly acute in the Kodagu district, which accounts for one-third of the Indian coffee production (Garcia et al., 2010), and is located in the Western Ghats biodiversity hotspot. Kodagu district landscape has strongly evolved over the last decades, with an important rate of forest degradation and deforestation due to coffee estate expansion toward the western forested area (Lo Seen et al., 2010), and the introduction of the fast-growing species *Grevillea robusta* in the canopies of coffee AFS (Garcia et al., 2010; Nath et al., 2016). The natural distribution area of *G. robusta* is located in Australia, but this species has been introduced in a large part of Asia and in Africa, where it is considered as an exotic species (http://www.worldagroforestry.org/treedb2/). Farmers' preference for *G. robusta* in the Western Ghats is thought to be mainly driven by the economic and legal advantages conferred on it by the existing policy framework, even though native trees have higher multipurpose utility and potential economic value (Garcia et al., 2010; Nath et al., 2016). Exotic species can indeed be harvested freely whereas native species require official permit to be harvested, which may not be granted under certain forms of land tenure where the government claims ownership rights over current and future native trees (Garcia et al., 2010; Nath et al., 2016). As a consequence, *G. robusta* was replanted five time more often than native trees over the 2011–2016 period in coffee AFS of the Western Ghats (Nath et al., 2016). Furthermore, coffee plants of the area have undergone pest attacks (stem borer, *Xylotrechus quadripes*) that have led farmers to convert their Arabica coffee (*Coffea arabica*) plantations into more resistant Robusta coffee (*Coffea canephora*) plantations (Garcia et al., 2010). The consequences of these management changes for C storage and biodiversity of the Western Ghats remain however poorly documented.

Kodagu district has extremely contrasted ecological conditions, with mean annual precipitation (MAP) ranging from 1200 mm in the East to more than 5000 mm in the West within about 50 km (Fig. 1). Such environmental gradients can be advantageously used to study the response of AFS to changes in precipitations, which integrate both the responses of plant functioning and farmer's management to contrasted environmental conditions. Therefore, it is possible to study synergies, antagonisms and trade-offs among the ecosystem services provided by AFS in contrasted environmental contexts. In this study, we aimed at quantifying how C storage and tree shade diversity vary among land-use systems (from native forest, to native shade tree AFS, to exotic shade tree AFS) along a 3500 mm MAP gradient in the Kodagu district. Moreover, we additionally aimed at quantifying the impact of Arabica to Robusta conversion in terms of C storage and tree shade diversity in this area.

We specifically tested the following hypotheses: 1) the management of AFS (planting of exotic trees in AFS, selective logging and pruning in native AFS) decreases C storage and tree species diversity compared to native forest; 2) the introduction of the fast-growing species *G. robusta* in AFS increases above-ground C storage compared to native AFS, but decreases soil C storage because of a reduction in soil biological activity; and 3) carbon storage and tree diversity are lower in Robusta coffee than in Arabica coffee AFS, as the higher light and high temperature tolerance of Robusta coffee plants allows for a low canopy density management. The impacts of our findings for management guidelines and conservation policies of coffee AFS in the Indian Western Ghats were discussed in a concluding section.

2. Materials and methods

2.1. Study area and sample design

The study area was the Cauvery watershed zone of the Kodagu district, Karnataka state, India (Fig. 1). Altitude ranges from 850 m in the East of the district to 1875 m in the West. Precipitation is strongly seasonal, with a maximum occurring during the monsoon, between June and August (Elouard and Guilmoto, 2000). Mean annual precipitation ranges from 1200 mm to more than 5000 mm within about 50 km from East to West. Forest cover of the study area is comprised of "low elevation wet evergreen forests" in the West and "moist to dry deciduous forests" in the East (Elouard and Guilmoto, 2000).

The watershed was surveyed in order to find locations with a native forest patch close to an AFS with native shade trees (called hereafter "native AFS") and / or close to an AFS with exotic shade trees ("exotic AFS"). Study plots were then established in each land-use system, in such way that i) plots were at a maximum distance of 300 m from each other, and had comparable topographical and soil characteristics (especially soil texture, Table 1) ii) native tree species represented more than 90% of the shade tree basal area in native AFS plots, and *Grevillea robusta* represented more than 60% of the shade tree basal area in exotic AFS plots.

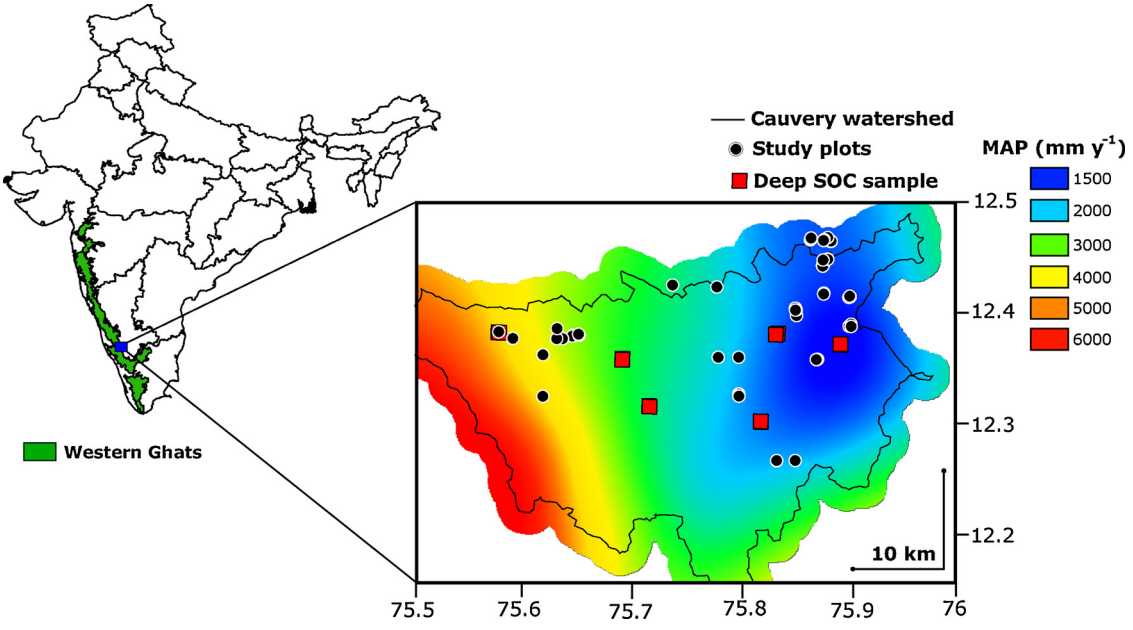

Fig. 1. Locations of the study sites, throughout the Cauvery watershed (Kodagu district, Karnataka state, India). MAP: Mean annual precipitation; SOC: Soil organic carbon.

Table 1
Study site characteristics. Values with the same letter were not significantly different within a precipitation zone (no comparison was made between precipitation zones, no letters were shown when there was no difference among land-use systems). *n* is the number of sites, MAP is mean annual precipitation, AFS is agroforestry systems. Total sampled area is the sum of the areas of all the plots included in each land-use system category. Stem density, stem basal area and canopy closure were measured for the shade trees only (excluding coffee plants). The moderate and the high precipitation zones comprise sites with mean annual precipitation lesser and greater than 3000 mm y^{-1}, respectively.

	Moderate precipitation					High precipitation		
	Forest	Native AFS		Exotic AFS		Forest	Native AFS	Exotic AFS
		Robusta	Arabica	Robusta	Arabica		Robusta	Robusta
n	14	12	7	11	6	4	8	5
Total sampled area (ha)	0.99	0.85	0.49	0.78	0.42	0.28	0.56	0.35
Altitude (m)	941	946	933	935	934	948	936	941
MAP ($mm.y^{-1}$)	1736	1753	1549	1755	1598	3760	3834	3597
Temperature (°C)	22.0	22.0	22.2	21.9	22.3	21.8	21.8	21.8
Soil clay content (%)	14.2	14.7	13.3	14.7	10.5	15.7	13.5	14.4
Soil bulk density ($g.cm^{-3}$)	1.4	1.43	1.42	1.39	1.38	1.33	1.32	1.39
Fine soil fraction (%)	84	90	90	88	88	69	64	62
Stand stem density (ha^{-1})	212^{a}	239^{a}	338^{ab}	319^{ab}	432^{b}	340^{a}	255^{a}	569^{b}
Stand basal area ($m^2.ha^{-1}$)	24.3^{a}	20.2^{ab}	24.7^{ab}	15.0^{b}	20.8_{ab}	17.4^{ab}	20.2^{a}	10.4^{b}
Canopy closure (%)	72.2^{a}	50.2^{b}	69.4^{a}	48.6^{b}	66.3^{a}	90.4^{a}	32.0^{b}	36.5^{b}
Number of coffee plants (ha^{-1})	n/a	1228^{a}	2180^{b}	1193^{a}	2119^{b}	n/a	953^{a}	978^{a}

For each plot, general information on the historical agricultural management was collected through interviews with farmers in order to ensure that it was under the same land-use system for more than 10 years (on average 26 years). We only selected mature stands (i.e. shade trees ready to harvest) and AFS with first-rotation coffee plants that had been implemented in native forest remnants. Mean annual precipitation estimates were obtained using a kriging procedure based on an original measurement database collected from local farmers (Supplementary information S1). Robusta coffee AFS were found throughout the watershed, while Arabica coffee AFS were found only in the Eastern, moderate MAP zone (Table 1). Overall, 67 plots were selected, which included 18 forest plots, 27 native AFS plots and 22 exotic AFS plots, gathered in 22 different locations (Fig. 1). Carbon stocks and shade tree diversity were surveyed in a 15 m-radius circle (i.e, ~700 m^2) located at least 20 m within the evaluated land-use system in order to reduce edge effects. Additionally to measurements undertaken in the 67 studied plots, deep soil organic C content was measured at six Robusta coffee AFS locations, throughout the Cauvery watershed (Fig. 1). The locations selected for deep SOC assessment, presented both exotic and native Robusta coffee AFS stands within a 300 m distance. Field assessment was conducted at the end of the dry season (February / March) in order to control for a potential effect of seasonal variation in leaf shedding on litter collection and ensure good sampling conditions for soil measurements.

2.2. Carbon storage and tree diversity surveys

For each plot, shade tree species diversity and the amount of organic carbon sequestered in woody above-ground biomass (AGB), root biomass, litter and soil were surveyed.

Circumference at breast height and total height of all shade trees with a circumference greater than 3 cm were measured (using a measuring tape and a Suunto® clinometer, respectively). All the measured trees were identified to species in the field by local experts. A small number of difficult species (< 2%), was identified only to genus. Tree shade AGB was then estimated using the generic allometric equation developed by Chave et al. (2014), and the ICRAF species-specific wood density database (http://db.worldagroforestry.org/wd).

Coffee AGB was estimated on the basis of local allometric equations calibrated for the purpose of this study (Supplementary information S2) using destructive sampling of Robusta ($n = 20$) and Arabica ($n = 25$) plants. Final models for Robusta ($P < 0.001$, $R^2 = 0.92$) and Arabica ($P < 0.001$, $R^2 = 0.97$) are presented in Eq. (1) and Eq. (2), respectively.

$$AGDM_{robusta} = 0.0177 \times C^{1.408} \times PCA^{0.818} \quad (1)$$

$$AGDM_{arabica} = 0.0048 \times C^{2.06} \times PCA^{0.525} \quad (2)$$

Where *AGDM* is above-ground dry matter (which includes trunk, branches and leaves, kgDM), *C* is circumference at 30 cm (cm) and *PCA* is projected crown area (m^2). Projected crown areas were estimated using 8 drip-line crown radius measurements per coffee, at well-distributed intervals on different sides of the crown. Projected crown areas were then calculated considering circular drip-line.

Biomass of coarse and fine roots (< 5 mm diameter) of both coffee and shade trees (below-ground biomass, BGB) was estimated using the root-shoot equation developed by Cairns et al. (1997, their Eq. (1)). Above and below-ground woody dry matter was then converted into amount of C by assuming a ratio of 0.5 (Tanabe and Wagner, 2003).

Litter was collected on 4 replications of a 1 m^2 area on each plot, carefully checked for soil particles, oven-dried for 48 h at 70 °C and weighted. Soil samples were collected in the central part of each plot at two depths (10 and 30 cm, 4 samples at each depth in cardinal directions) with a cylindrical auger. Soil bulk density, soil fraction finer than 2 mm and soil texture of each soil sample were measured (Bouyoucos, 1962). Litter and soil organic C content were measured on aliquots by a non-dispersive infrared sensor associated with a furnace (Total Organic Carbon V CSH-CSN and Solid Sample Module SSM 5000 A, Shimadzu Scientific Instruments). Soil organic C content (*SOC*, $MgC.ha^{-1}$) of a soil layer *i* (m) was then calculated as follows.

$$SOC_i = t_i \times OCC_i \times FF_i \times BD_i \quad (3)$$

where *t* is layer thickness (cm), *OCC* is organic C content ($gC.g^{-1}$), *FF* is fine soil fraction (%) and *BD* is soil bulk density ($g.cm^{-3}$). We considered a soil layer thickness of 20 cm, allowing in this case the estimate of SOC in the 0–40 cm horizon.

At each of the six Robusta coffee AFS locations selected for deep SOC assessment, exotic and native AFS were sampled with 2 replications in each land-use system at depth 10, 30, 50, 70, 90, 110, 130 and 150 cm (2 samples at each depth). SOC was estimated using the same procedure as described above.

Shade tree canopy closure was characterized on each plot with 8 densiometer measurements (Lemmon, 1956), using a systematic grid.

2.3. Data analyses

The dependency of C stocks and canopy closure to MAP was evaluated using models of decreasing complexity: power model, linear model and Wilcoxon signed-rank test. In this last case, we compared variable averages for high MAP (> 3000 mm) and moderate MAP (< 3000 mm). Model selection was based on likelihood-ratio tests. Differences in C stocks among land-use systems were explored using linear mixed models (LMMs, Zuur et al., 2009). We used LMMs to explore the dependencies of C stocks and study site characteristics (Table 1) to land-use systems (categorical variable: native forest, native Robusta AFS, native Arabica AFS, exotic Robusta AFS, exotic Arabica AFS). The location ID of the plots (all plots located within a distance of 300 m from each other shared the same location ID, see Section 2.1.) was introduced as a random effect on the intercept. This model formulation adds the assumption that observations within a location are correlated (covariance matrix with compound symmetry) and thus reduces the risk of bias in fixed effect inferences arising from spatial autocorrelation. LMMs were adjusted separately for total C stocks and each C stocks components, and for high (n = 33, 13 locations) and moderate (n = 34, 9 locations) MAP zones.

Shade tree diversity was evaluated through species richness (absolute species abundance), Pielou evenness index (relative species abundance), and Shannon index that accounts for both abundance and evenness of species (Ma, 2005). Species richness was evaluated in two ways: i) aggregated species richness that corresponds to the number of species observed when bringing together all the species observed for a particular land-use system and ii) plot species richness that corresponds to the number of species observed on average in our 15 m radius study plots. Tree diversity indices at plot scale were compared among land-use systems using LMMs by following the same procedure as described above for C stocks. We additionally ran non-metric dimensional scaling (NMDS) using the Bray-Curtis dissimilarity to analyse species composition changes (i.e. changes in species identities) between forest and Robusta AFS, and across the MAP gradient (Legendre and Gallagher, 2001). Only Robusta AFS data were included in this analysis, as Arabica AFS were not found in the high MAP zone. NMDS is an iterative, non-parametric ordination method that reduces large multivariate data into a few, interpretable axes. Correlations between NMDS ordination dimensions and environmental covariates were evaluated based on data permutation tests (*envfit* function of the vegan R package), using squared correlation coefficient (r^2) as the goodness-of-fit statistic. All the models were adjusted using the R software (RcoreTeam, 2016), with 5% significance level. LMMs were adjusted using the nlme R package (Pinheiro et al., 2014), and diversity index and NMDS calculation were performed using the vegan R package (Oksanen et al., 2013).

3. Results

The soil textures of the selected plots ranged from “loamy sand” to “sandy loam” and to “sandy clay loam”. Soil characteristics (texture, bulk density and fine soil fraction), MAP and mean temperature did not significantly differ among land-use systems (i.e. comparing forest vs native AFS vs exotic AFS), within both moderate and high precipitation zones (Table 1). The measured canopy closure was on average significantly lower in Robusta AFS than in Arabica AFS (comparison made in the moderate MAP zone, Table 1). Strikingly, canopy closure of forest and AFS displayed much contrasted trends along the MAP gradient (Fig. 2A) as forest canopy closure increased with MAP until a saturation level close to 90% whereas canopy closure of both native and exotic AFS decreased steadily to reach low levels (< 40%) in the high MAP area. Averaged shade tree AGB of AFS plots displayed little change along the MAP gradient (Fig. 2B) whereas a significant decrease in forest shade tree AGB was reported in high MAP area.

A pool of 86 native tree species was identified, with the four most common species being *Acrocarpus fraxinifolius*, *Ficus racemosa*, *Erythrina suberosa* and *Dalbergia latifolia*. Aggregated species richness reached a maximum value in the forest remnants of the moderate precipitation zones (45 species, Table 2) and a minimum value in the exotic Robusta coffee AFS of the high precipitation zone (9 species). Shade tree species diversity, as measured by plot species richness and Shannon index, had comparable values in forest and native AFS plots throughout the MAP gradient (Table 2), while it was significantly lower in exotic AFS. The Bray-Curtis dissimilarities also revealed that the tree species communities of native AFS differed significantly, although moderately ($r^2 = 0.12$, $P < 0.01$), from the species communities of native forests over the studied area (Fig. 3). The most predominant driver of species composition changes was the MAP ($r^2 = 0.53$, $P < 0.01$, Fig. 3), which highlights important species community shift from the dry East to the moist West of the watershed. Contrastingly, tree species evenness was unaffected by changes in land-use system (Table 2).

Total C stocks (with SOC measured down to 40 cm depth) observed in the Cauvery watershed ranged from 146 to 367 MgC ha^{-1} (average of 222 MgC ha^{-1}), and from 106 to 327 MgC ha^{-1} (average of 193.1 MgC ha^{-1}), for forests and coffee AFS, respectively (values per MAP zones, land-use system and C stock components are given in Supplementary information S3). Soil organic C (0–40 cm) was the main C stock in forest, native and exotic AFS, accounting for 45%, 47% and 54% of total C stocks, respectively (Fig. 4). It was followed by above-ground shade tree C accounting for 43%, 37% and 30% of total C stocks in forest, native and exotic AFS, respectively. Above-ground C stocks had comparable values in forest and native AFS while it decreased significantly in exotic AFS, in both moderate and high MAP zones (Fig. 4). Total C stocks of Robusta coffee AFS with exotic shade trees was significantly lower than all other land-use systems in both precipitation zones (Fig. 5).

Deep SOC (40 cm–160 cm depth) in Robusta AFS differed among sampled plots (P = 0.03), but was comparable between exotic and native AFS (Supplementary information S4), and was not related to MAP. The significance of the plot effect for deep AFS SOC was attributable to one plot located at MAP = 2079 mm, where we observed two SOC profiles out of 4 with very low values (Supplementary information S4, Fig. S4c). Overall, deep SOC accounted for 43 ± 9% of the total SOC in Robusta AFS, with an average C stock value of 70 ± 28 and 65 ± 21 MgC ha^{-1} in the high and moderate precipitation zones, respectively.

There was a significant and positive correlation between tree species diversity (quantified using Shannon index) and total C stocks, across native forest, native AFS and Exotic AFS in the studied coffee agroforestry landscape (Fig. 5). This positive correlation was consistent across both Robusta and Arabica systems, and across both moderate and high MAP zones.

4. Discussion

4.1. Carbon stock estimation

Numerous bias and differences in methodologies can affect C stock estimation, comparison and interpretation in forests and AFS (Albrecht and Kandji, 2003). In this study, leaf and root biomass were not directly quantified in the field, which is one of the methodological limits of our work. Rather, leaf biomass was neglected (it usually represents less than 5% of total C stocks; Körner, 1994) and root biomass was estimated using allometric equations. Contrary to coarse roots, leaves and fine roots are high-turnover organs, whose contribution to C storage cannot be reduced to existing C stocks at a given point in time (Gill and Jackson, 2000). Leaves and fine roots indeed represent significant C sinks (Brüggemann et al., 2011) that ultimately feed C litter and upper soil horizons. On the long-term and in quasi-equilibrium state, the impact of land-use changes on leaves and fine roots will therefore be partly reflected in the amount of leaf litter and SOC that was observed

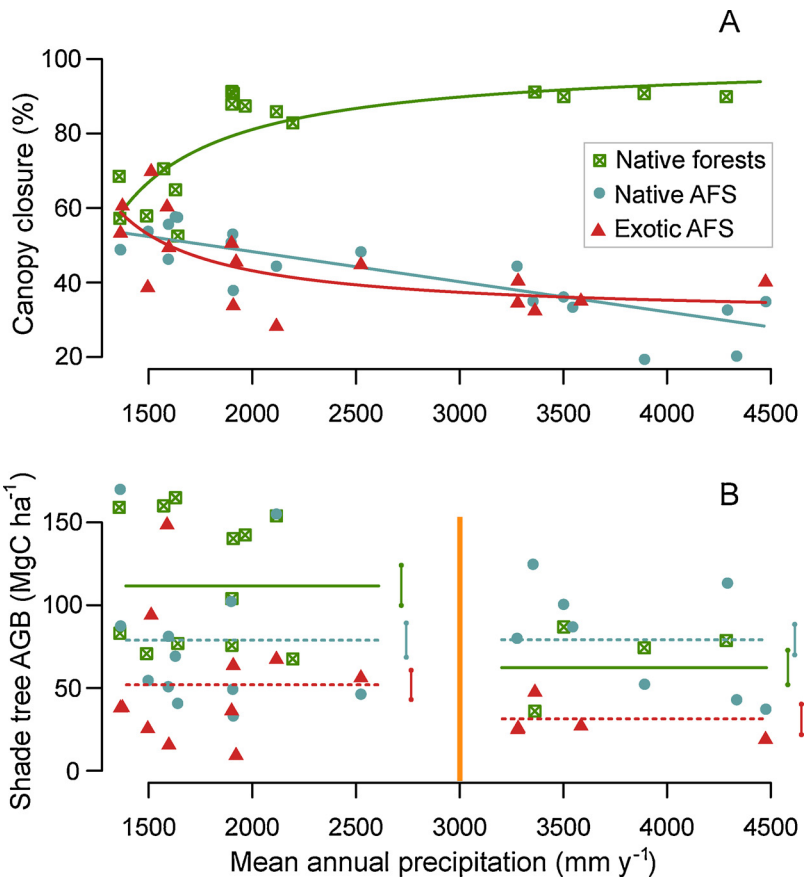

Fig. 2. Changes in canopy cover (A) and tree above-ground biomass (B) along a 3500 mm precipitation gradient for three land-use systems of a Robusta coffee agroforestry landscape in the Western Ghats of India. A: Native forests (power model, $R^2 = 0.41$, $P < 0.001$); Native AFS (linear regression, $R^2 = 0.71$, $P < 0.001$); Exotic AFS (power model, $R^2 = 0.33$, $P < 0.01$). B: the precipitation gradient was divided in two zones (greater and lesser than 3000 mm/y). Dashed lines indicate no statistical difference between the high and moderate precipitation zones ($P > 0.05$). Vertical bars are standard errors. AFS: Agroforestry system; AGB: Above-ground biomass.

Table 2
Shade tree diversity in coffee agroforestry systems (AFS) and native tropical forests. Values with the same letter were not significantly different within a precipitation zone (no comparison was made between aggregated species richness values). Aggregated species richness corresponds to the number of species observed when bringing together all the species observed for a particular land-use system. Plot species richness corresponds to the number of species observed on average in our 15 m radius study plot. The moderate precipitation zone and the high precipitation zones comprise sites with mean annual precipitation lesser and greater than 3000 mm y^{-1}, respectively.

	Moderate precipitation					High precipitation		
	Forest	Native AFS		Exotic AFS		Forest	Native AFS	Exotic AFS
		Robusta	Arabica	Robusta	Arabica		Robusta	Robusta
Aggregated species richness (# species in all plots)	45	44	24	11	12	29	37	9
Plot species richness (# species in a 15m-radius circle)	7.2[a]	7.5[a]	6.9[a]	3.8[b]	4.8[b]	10.5[a]	9.3[a]	4.2[b]
Pielou evenness index (unitless)	0.26[a]	0.24[a]	0.22[a]	0.18[a]	0.19[a]	0.26[a]	0.24[a]	0.19[a]
Shannon index (unitless)	1.77[a]	1.70[a]	1.39[a]	0.62[b]	0.88[b]	2.08[a]	2.01[a]	0.52[b]

at the different plots (Schmidt et al., 2011). However, SOC is not solely determined by leaves and roots litter inputs and soil biological activity but is affected as well by changes in soil bulk density (De Beenhouwer et al., 2016) together with soil texture, especially clay content (Grüneberg et al., 2013). By selecting plots with at least 10 years of homogeneous management and by controlling for soil density and texture discrepancies among plots, we aimed at reducing risks of biased interpretations and providing sound C stocks estimates. However, limits of our approach has to be underlined; as an important example, soil aggregate fractions, which may have an influence on the mean soil C residence time in the various land-use systems (Six et al., 2000), was not measured.

In line with literature (Parry et al., 2007), SOC in the 0–40 cm horizon was the main C stock in forest, native and exotic AFS, followed by tree above-ground C stock. While we report that in some instances SOC at 0–40 cm differed among land-use systems, deep SOC (40–160 cm) was similar between native and exotic AFS throughout the watershed (Supplementary information S3). This is in line with a recent meta-analysis indicating that deep soil carbon (> 20 cm) dynamics are driven more by soil type than by climate or vegetation type (Mathieu et al., 2015). However, the land-use conversions at our study plots may be too recent (10–30 years) to detect land-use effects on deep SOC. Deep SOC accounted for 43 ± 9% of total SOC profiles over the 6 sampled plots, which is coherent with values from a previous meta-analysis (Jobbágy and Jackson, 2000) and confirms that a substantial part of the soil C is accounted for in the present study. Overall, the total C stocks (with SOC measured down to 40 cm) that we report here for AFS (maximum average for native Arabica AFS at 228 MgC ha^{-1}) are

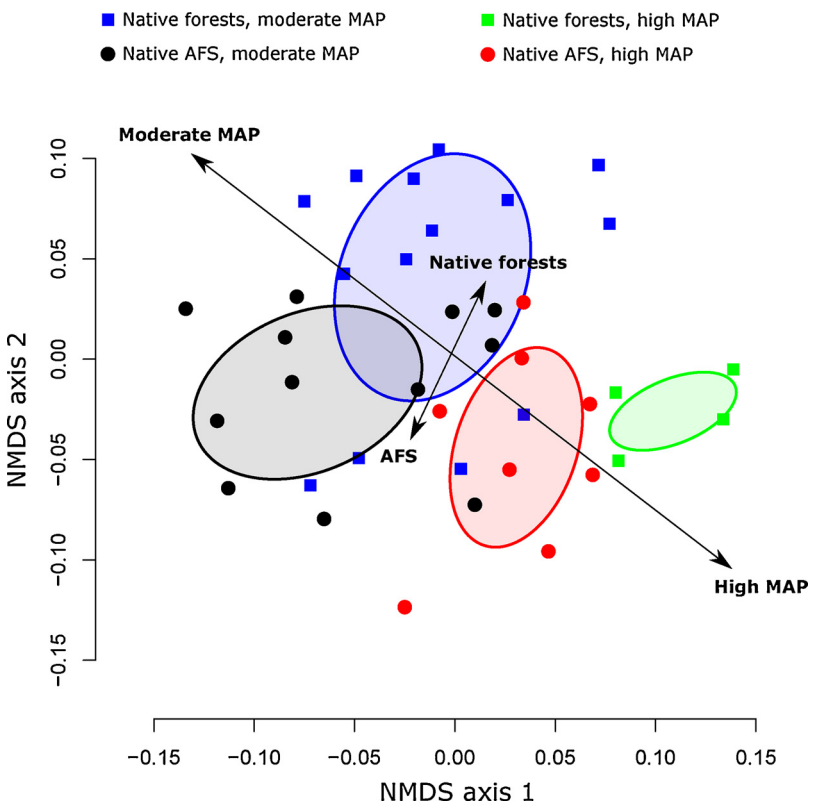

Fig. 3. NMDS analysis of the tree diversity composition of native AFS and forests in a Robusta coffee agroforestry landscape of the Western Ghats of India. The NMDS analysis was based on Bray-Curtis dissimilarity index. The NMDS axes correspond to the 2-dimensional ordination that maximized the consistency between dissimilarities in the original matrix and dissimilarities in the reduced ordination matrix. Arrow lengths are proportional to the goodness-of-fit (squared correlation coefficient) of the environmental variables with the ordinate data (Mean annual precipitation, $r^2 = 0.53$, $P < 0.01$; Land-use system, $r^2 = 0.12$, $P < 0.01$). Each point corresponds to one study plot. Colours distinguish land-use systems and MAP zones. MAP: Mean annual precipitation; AFS: Agroforestry system. Data from Arabica AFS were excluded from this analysis, as this system was not found in the high MAP zone.

high but coherent when compared to the C storage potential of agroforestry systems worldwide (Albrecht and Kandji, 2003; Nair et al., 2009).

4.2. Management impacts on C storage

Forest and AFS displayed contrasted canopy closure responses to MAP changes, which indicates that farmers of the Cauvery watershed finely manage AFS leaf area in function of local climate conditions (Fig. 2). Differences of shade levels between AFS and forests could have resulted from the changes in species composition observed in AFS compared to forests, but also from changes in stand structure through planting, thinning and pruning that were reported as common practices during farmers' interviews conducted in this study. It is likely that the strong decrease in AFS canopy closure with increasing MAP resulted from the need to increase coffee light availability in humid zones with

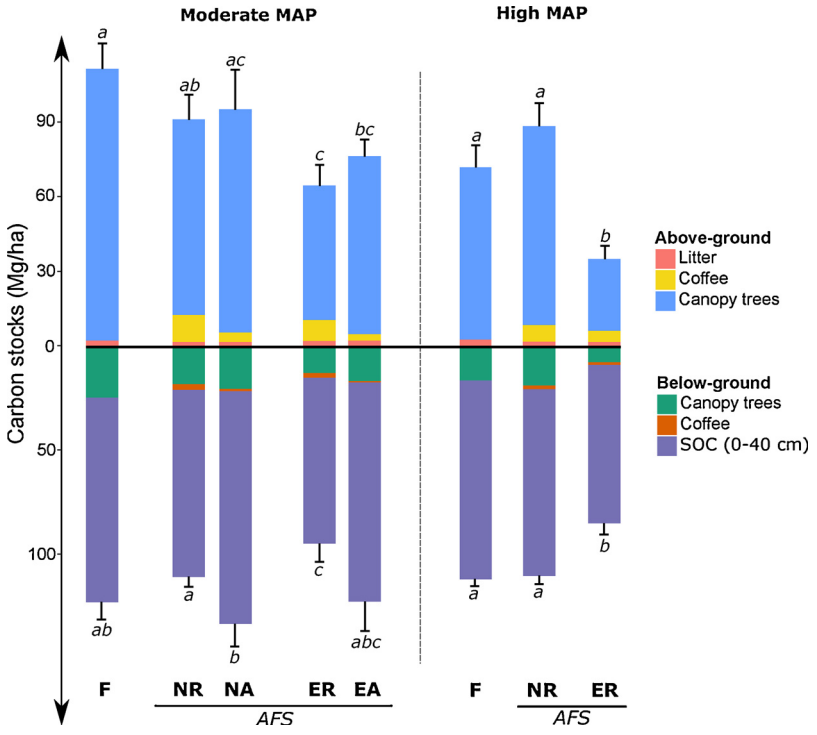

Fig. 4. Carbon stocks of exotic and native coffee AFS, as compared to native forests in a coffee agroforestry landscape of the Western Ghats of India. Values with the same letter were not significantly different within a precipitation zone (no comparison was made between precipitation zones). AFS: Agroforestry systems; F: Native forests, MAP: Mean annual precipitation, NA: Arabica-based native AFS; NR: Robusta-based native AFS; EA: Arabica-based exotic AFS; ER: Robusta-based exotic AFS, SOC: Soil organic carbon.

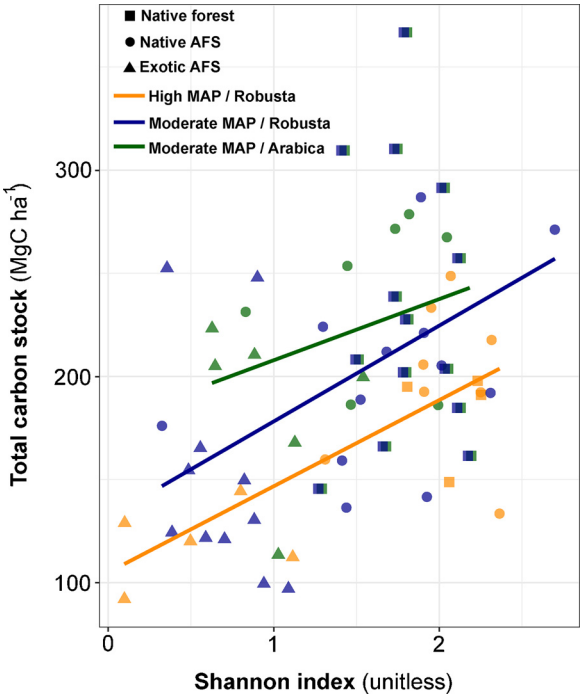

Fig. 5. Relationship between shade tree diversity (Shannon index) and total carbon stocks across three land-use systems of a coffee agroforestry landscape in the Western Ghats of India. Total C stock estimates were obtained by summing litter, coffee and shade tree above-ground carbon stocks, soil organic carbon content (0–40 cm) and coffee and shade tree below-ground C stocks. Changes of carbon stocks and tree diversity among land-use systems (native forests, native AFS and exotic AFS) are presented for Robusta in the high (yellow, n = 17) and moderate (blue, n = 37) MAP zone and Arabica in the moderate MAP zone (green, n = 27). Lines are linear regression models, all three regressions were significant ($P < 0.05$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

overcast skies and hence low solar radiation, in order to enhance photosynthesis and productivity. Accordingly, annual precipitation was strongly related to cloudiness and solar radiation of the rainy season (May to September) across our 67 study plots ($P < 0.001$, $R^2 = 0.96$, Supplementary information S1). Even though changes in light-use efficiency have been shown to partly compensate for the decreased light interception of shaded coffee plants (Charbonnier et al., 2017), the tuning of tree shade could be a predominant management target in order to sustain high coffee productivity in high MAP areas. Alternatively, the observed opening of tree canopy in high MAP areas could be ascribed to the necessity for managers to reduce the risk of pest attack and fungal diseases, as lower temperatures and higher air humidity under trees can foster parasitism and fungus development (Staver et al., 2001). We additionally report that tree canopy closure was significantly lower in Robusta AFS than in Arabica AFS. This is in line with the reported higher ability of Robusta plants to sustain productivity under high temperature and high water vapour deficit than Arabica plants (DaMatta, 2004) and thus to benefit more from direct sun exposition (Lin, 2007).

The conversion of forest or native AFS to exotic AFS, i.e. to the replacement of many native trees by *G. robusta* trees, led to a significant decrease of C stocks throughout the study area. This result contradicts the view of exotic plantations being advantageous in terms of C offsetting and climate change mitigation compared to native stands (Lindenmayer et al., 2012). However, the potential of the different land-use systems for C storage has to be evaluated considering the whole carbon cycle, including differences in rotation length and wood product's life cycle (Helin et al., 2013). In order to reduce possible bias arising for differences in rotation length among land-use systems, we only selected stands thought to be mature (i.e. at the end of the shade tree rotation cycle) by farmers. We consequently measured and compared the maximum amount of C stored in each land-use system under the management standards and environmental conditions of our study area, which is a proxy of the potential of such systems to mitigate climate change, particularly with respect to precipitation regime. Moreover, two studies undertaken in the study area showed that *G. robusta* and the native trees commonly found in native AFS have comparable average growth rates (Garcia et al., 2010; Nath et al., 2016). This means that native and exotic AFS are unlikely to differ in terms of C storage efficiency, even though differences in wood density among species should be considered as well. Finally, native trees have significantly higher economical values than *G. robusta* (Nath et al., 2016), which is likely related to the production of long-lasting wood products such as furniture, and hence long-lasting C storage (van Kooten and Johnston, 2016). Therefore, our result is probably conservative and underestimates the decrease in C storage that is linked to the conversion of forest or native AFS to exotic AFS on the long run.

We report a decrease in C stocks of both the above-and below-ground components of exotic AFS, compared to native AFS and forest. Changes in above-ground C stocks among land-use systems were likely caused by important changes in structure, especially a strong decrease of stand basal area in exotic AFS compared to native plots (Table 1). We note that although Robusta coffee plants accumulated significantly higher amount of C than Arabica plants, this was not sufficient to change the overall pattern of reduction of C stocks in Robusta coffee AFS, which was mainly driven by changes in shade tree biomass (Fig. 4, Supplementary information S3). The diminution of below-ground C stocks in exotic AFS was mainly driven by the reduction of SOC, which suggests that the quality and / or quantity of soil litter inputs from *G. robusta* are less favourable to decomposition processes and soil biological activity than native tree litter. This is in line with previous studies showing a lowering of soil biological activity after the introduction of exotic tree species in native stands (Castro-Díez et al., 2012), including a work conducted in coffee AFS of the study region (Bagyaraj et al., 2015). Overall, it is likely that the reduction of C stocks in exotic AFS was mainly driven by changes in stand structure (resulting from management choices) and by the functional characteristics of *G. robusta* compared to native species. However, changes in tree species diversity *per se* could also partly have caused the differences in C stocks that were observed among land-use systems, as tree diversity was shown to affect most of forest ecosystem functions, from tree productivity to soil biological activity and water cycling (Bardgett and van der Putten, 2014; Potvin and Gotelli, 2008). The effect of tree diversity on AFS functioning and C stocks was not possible to isolate based on our dataset, but constitutes an interesting topic for future research.

4.3. Shade tree diversity and C storage

The species richness of native AFS observed when aggregating all inventories was higher (reaching a maximum of 44 observed species in the moderate precipitation area) than many other coffee landscapes worldwide (Nath et al., 2016). Tree species diversity, as measured by plot species richness and Shannon index, had comparable values in forest and native AFS plots throughout the MAP gradient, but decreased significantly in exotic AFS for both Robusta and Arabica systems. Native AFS accordingly displayed aggregated species richness comparable to forest observed in this study and in previous works conducted in the Western Ghats (Ayyappan and Parthasarathy, 1999). By contrast with species richness, evenness did not differ among land-use systems in our study, which is surprising as a disproportionate number of *G. robusta* was expected in exotic AFS. This result is likely due to the small girth threshold (3 cm) that we used for tree detection in our inventories, which led to include in the inventories a high number of small native trees growing in the understorey of exotic AFS.

Our results suggest that native AFS of the studied region allow growing coffee while maintaining a tree cover that shares both the structure (C stocks, stem density, stand basal area) and the tree diversity of neighbouring forest, despite a small shift in their species communities (Table 1, Fig. 3). It is thus likely that native coffee AFS of the Kodagu district provide forest-like habitats for a wide range of species and act as biodiversity conservation areas (Garcia et al., 2010) comparable to neighbouring forest. In agreement with this result, De Beenhouwer et al. (2016) and Steffan-Dewenter et al. (2007) reported minor biodiversity changes between forest and extensive native AFS, despite substantial changes in shade tree cover.

Despite a substantial reduction of shade tree cover in native AFS compared to forest (from 90% to 32% in the high precipitation area), native coffee agroforestry of the study area conserved C stocks and tree diversity comparable to forest throughout a 3500 mm MAP gradient. Moreover, our data suggest that both C stocks and tree diversity were negatively affected by the introduction of *G. robusta* in AFS. Consequently, tree diversity and C storage positively co-varied in the coffee agroforestry landscape of the Indian Western Ghats (Fig. 5). Such a positive correlation between ecosystem services in coffee AFS has also been reported in two studies led in Central America (Häger, 2012; Richards and Mendez, 2014). The negative impact of exotic coffee agroforestry on C stocks was higher for Robusta than for Arabica systems. This result highlights that the management responses to the different requirements of both species in terms of temperature and light exposure, that lead to higher canopy opening in Robusta coffee systems, affects the ecosystem services provided by coffee AFS.

4.4. Implications for coffee AFS management in the Western Ghats

Our data suggest that the current trend toward the introduction of *G. robusta* in coffee AFS canopies, as well as the conversion of Arabica to Robusta systems, have a negative impact on both climate change mitigation potential (through the reduction of C storage) and tree diversity conservation in the Western Ghats. Garcia et al (2010) and Nath et al. (2016) showed that the current preference for exotic agroforestry in the Western Ghats is mainly driven by the economic and legal advantages conferred on this exotic species by the existing policy framework. It is interesting to note that the economic advantage of *G. robusta* seems not to arise from higher growth rate or higher value per unit volume in the market than native trees, but rather from the fact that farmers are able to legally sell higher volumes of exotic species on the open market (Garcia et al., 2010; Nath et al., 2016). Recent initiatives to support and expand agroforestry in India, such as the National Agroforestry Policy (Chavan et al., 2015), have therefore the opportunity to efficiently foster climate mitigation and tree diversity conservation by addressing legal obstacles toward the economical valorisation of native AFS trees. In line with this statement, two out of the four most common species in our native AFS species survey (*A. fraxinifolius*, and *D. latifolia*) are considered by farmers to be of high multipurpose utility value and highly valuable timber trees (Nath et al., 2016).

5. Conclusion

Financial mechanisms could take advantage of the carbon-tree diversity positive correlation reported here in the coffee agroforestry landscape of the Western Ghats of India to promote conservation and climate change mitigation. Notably, our results support the view that mechanisms for conserving biomass (such as the REDD + mechanism) would have substantial co-benefits for AFS tree diversity. Conversely, market-based promotion of biodiversity (Pirard, 2012), e.g. based on payment for ecosystem services or forest certification, would enhance AFS carbon storage as well as climate change adaptation and mitigation (Vaast et al., 2016). Finally, beyond the co-benefit of C storage and tree diversity in native AFS reported here, financial incentive systems could support native AFS coffee production (Marie-Vivien et al., 2014) as coffee bean quantity and quality were shown to be enhanced for coffee plant grown under diverse shade tree canopy (Nesper et al., 2017). The conservation of tree diversity and C stocks in the Western Ghats needs a flexible and participatory approach, considering farmers' perceptions of trees and forests, economic and ecological requirements (Pfund et al., 2011). In this perspective, the promotion of native AFS is one of the leverage that should be used to reconcile agricultural production, biodiversity conservation and C storage in the region.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agee.2018.06.002.

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